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BIODIVERSITY RESEARCH

When is a species really extinct? Testing extinction inference from a sighting record to inform conservation assessment

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ABSTRACT

Aim The global extinction of a species typically represents the end point in a series of population extinctions, during which unique evolutionary history is lost at every stage. Insight into the process of extinction can provide the means to identify species at high risk, but the number of extinctions being identified languishes far behind true totals. More proactive ways of inferring extinction from limited data are required.

Location Historic sightings, collections and specimen data from Australia and Asia.

Method We used a technique called optimal linear estimation to analyse the sightings record of mammal and bird species of varying ecology, life history and population demography. The mammal species chosen were all considered regionally extinct in the literature, while the bird species chosen had all been highlighted as candidates for the new IUCN Red List category flag: Critically Endangered (Possibly Extinct).

Results Nine of the ten mammal species were predicted to be probably extinct, but only two with 95% certainty. Seven of the ten bird species were predicted to be probably extinct, four with 95% certainty.

Main conclusions Superficially, determining whether a species is extinct might seem a simple task, whereby we either find a species extant, or it is extinct. In reality, however, the task is much more complex. Techniques such as optimal linear estimation, in combination with other data sources, and knowledge of recording effort, may prove useful in inferring extinction across a variety of taxa but should not be used in isolation.

Keywords

Extinction, IUCN, optimal linear estimation, population decline, possibly extinct, time series.

INTRODUCTION

The global extinction of a species typically represents the end point in a series of population extinctions, during which unique evolutionary history is lost at every stage (Pimm *et al.*, 1988; Ceballos & Ehrlich, 2002). The loss of the final individual of a species represents the irretrievable loss of a unique form of biodiversity (Diamond, 1985, 1987). Insight into the process of extinction can provide the means to identify species at high risk and highlight groups or regions that may be particularly extinction prone (Pimm *et al.*, 1988; Purvis *et al.*, 2000a; Baillie *et al.*, 2004; Millennium Ecosystem Assessment, 2005).

The severity of the extinction crisis is often expressed in terms of counts of extinct species, with lengthening lists representing continuing loss of biodiversity, whereas the lack of addition to such lists could be seen as an indicator of conservation success (Keith *et al.*, 2004). The rate of extinction of species and the length of lists of extinct species are two markers by which conservation practitioners can gauge the success or failure of their actions. Other measures may be more responsive and relevant (Balmford *et al.*, 2003), but species

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extinction retains a central position in the assessment of biodiversity loss. Although the techniques used to estimate extinction have improved and data on extinction have become more readily available, there remains significant uncertainty in assessing species extinction rate. This is partly because of the difficulties in measuring extinctions in undescribed taxa and partly because establishing when the last surviving individual of a species has finally died remains problematic. The distinction between being very close to extinction, functionally extinct (too few individuals to sustain a viable population) and extinct is a difficult one to draw (Butchart *et al.*, 2006). Eight hundred and four extinctions have been documented since 1500 AD (IUCN, 2009), but this is certainly a considerable underestimation of the true extent of extinction during this period (Turvey, 2009).

Extinction is rarely witnessed so must be inferred (Diamond, 1987). If it is not possible to do this in an unbiased manner, then views of biodiversity patterns are correspondingly distorted. Scientists are reluctant to state with certainty if a species is extinct, so as not to facilitate the Romeo effect (giving up on a species too early; Collar, 1998) or the Lazarus effect (bringing species back from being named extinct; Keith & Burgman, 2004). In essence, there needs to be a decision on the length of time or the amount of searching required without sighting a species in order for it to be confidently considered extinct. The ramifications of getting it wrong can be far reaching. For example, the recent claimed rediscovery of the ivory-billed woodpecker (*Campephilus principalis*) in the Big Woods region of Arkansas (Fitzpatrick *et al.*, 2005) led to the immediate allocation of $10 million by US Department of the Interior and Department of Agriculture for projects to conserve the bird and its habitat (Wilcove, 2005). Conservation funds are, understandably, not targeted at species thought to be extinct (Butchart *et al.*, 2006). With only limited funds to be divided among the deserving causes, the decisions had implications for many other species. Further, rapid taxonomic change because of species inflation represents a problem for lists of threatened and extinct species. Many subspecies are being elevated to specific level because of a change in species concept rather than new discovery (Hey, 2001; though see Sangster, 2009). For potentially extinct species, such changes make tracing back sighting records problematic, as it can become increasingly unclear which taxon was recorded. Conservation biologists must therefore be cautious about their dependency on such lists as accurate biodiversity indicators (Isaac *et al.*, 2004).

Determining whether a species is extinct through extensive survey work may be prohibitively costly, and expert opinion may involve considerable subjective bias (van der Ree & McCarthy, 2005), so more cost-effective and robust alternatives must be sought. The technical difficulty in discriminating species extinction lies in answering the question: how long should a species go unseen before we can safely call it extinct (Solow, 2005)? The answer is not simple and depends on the expected rate at which a species would be seen if it were extant. Calculating this for very poorly known taxa is yet more complex. IUCN guidelines state a species should be considered extinct when ''there is no reasonable doubt that the last individual has died'' and that this is reliant on ''exhaustive surveys in known and/or expected habitat, at appropriate times… throughout its historic range'' (IUCN, 2001). To avoid the Romeo effect and its potential to prohibit the implementation of conservation actions for the most extinction-prone species, IUCN deliberately places the burden of proof on evidence that the species is not present (Mace *et al.*, 2008). However, this may not be an appropriate bias when the objective is to assess extinction risk in a consistent manner.

The problem is analogous to that of estimating time of extinction of a species from its last occurrence in a stratigraphic sequence (see Collen & Turvey, 2009). It was long assumed that mass extinctions could be read directly from the fossil record. However, because of the vagaries of the fossil record (taxonomic, temporal and geographic incompleteness) and varying collection effort, it is difficult to reliably infer extinction. Observed stratigraphic ranges are likely to be an underestimate of true range (Benton, 1994), and a number of techniques have been developed to statistically infer true stratigraphic boundaries (e.g. Strauss & Sadler, 1989; Marshall, 1994; Solow & Roberts, 2003). Conservation biologists likewise require methods that can reliably conclude whether or not a taxon is extinct from very limited data sets among data that are inconsistent in sampling effort and in taxon population size. A number of techniques have been proposed, principally by Solow (2005), to attempt to make more quantitative the current qualitative process of classifying species as extinct.

While the current precautionary approach towards the classification of extinction is reasonable given the likely repercussions of getting it wrong, underestimating the number of extinct species will nevertheless bias analyses of extinction towards conservative estimates of human impact. Therefore, it is appropriate that techniques that offer a more objective and quantitative assessment of extinction are tested. The method used in this study comes from a technique called optimal linear estimation (OLE: Cooke, 1980), herein referred to as Cooke's estimator, a nonparametric method that allows extinction date to be estimated based on the distribution of the most recent sightings. This type of analysis has the possibility of providing a quantitative check on what is often a qualitative process of inferring extinction, on limited data that are frequently the only information available. Methods based on Cooke's estimator appear to offer good results (Solow, 2005) but have not been widely tested among species. Parametric approaches have been shown to have high Type I error rates if their assumptions are not met, though they are likely to be more powerful when the assumptions are valid. We tested the utility of Cooke's estimator at two scales: globally and within a geographic region, among a range of species of differing ecology, body size and population demographies. We applied Cooke's method to collated sighting records of twenty vertebrate species to evaluate whether there is evidence that these species should be considered truly extinct. We address whether such techniques can be used to inform the Extinct and

newly proposed Possibly Extinct (Butchart *et al.*, 2006) categories of the IUCN Red List to tackle the current underestimation of extinct species.

METHODS

Data

Sighting records were collated for mammals considered regionally extinct in New South Wales and for Asian birds considered as candidate Possibly Extinct species by Butchart *et al.* (2006). These species were chosen in part pragmatically, because of availability of data, but also to maximize the range of ecology, body size, life history and population demography across the species set. The New South Wales Department of Environment and Conservation Wildlife Atlas (NSW Department of Environment & Conservation, 2005) was the primary source of information for mammals: data are compiled from a variety of sources including historical reports, survey data and the general public reporting sightings. While these data are extensive, they are nonetheless patchy and centred around areas of human habitation, along roads and tracks. However, any sightings of rare species within the state should be reported in this source, making it the most reliable available record of known sightings for New South Wales. It does not, however, account for sightings in the neighbouring states of Queensland, South Australia and Victoria. Ten Asian bird species were chosen from Butchart *et al.*'s (2006) list of candidates for Critically Endangered (Possibly Extinct). Sighting records were then compiled from the Asian bird Red Data Book (Collar *et al.*, 2001) and BirdLife's data zone (http://www.birdlife.org).

Analysis

The approach used to infer time of extinction is based on the Weibull distribution, a two-parameter model. Its origin is in weakest link analysis (Crawley, 2002); its use has traditionally been in engineering industrial risk analysis (for example, the failure of a component). The attraction for an analysis aimed at inferring extinction is because of the result that, provided the sample of sightings data are large enough (see Methods below), it is reasonable to assume that the k most recent sightings come from the same Weibull extreme value distribution, regardless of the parent distribution (Solow, 2005). We implemented the following from Solow (2005). The optimal linear estimate of time of extinction, $\hat{T}_E$, based on the k most recent sightings has the form:

$$\hat{T}_E = \sum_{i=1}^{k} w_i t_{n-i+1} \tag{1}$$

The weight vector $w = (w_1, w_2, \ldots, w_k)'$ is given by:

$$w = (e'\Lambda^{-1}e)^{-1}\Lambda^{-1}e \tag{2}$$

where e is a vector of k 1's and Λ is the symmetric k-by-k matrix with typical element:

$$\Lambda_{ij} = \frac{\Gamma(2\hat{\nu}+i)\Gamma(\hat{\nu}+j)}{\Gamma(\hat{\nu}+i)\Gamma(j)} j \le i \tag{3}$$

where Γ is the gamma function and

$$\hat{\nu} = \frac{1}{k-1}\sum_{i=1}^{k-2} \log\frac{t_n - t_{n-k+1}}{t_n - t_{i+1}} \tag{4}$$

is an estimate of the shape parameter of the Weibull extreme value distribution, where t_n is the n times a species is sighted during an observation period t. Last, under the assumption that the species is extinct, the upper bound of an approximate 1 - α confidence interval for $\hat{T}_E$ is

$$T_E^u = \frac{t_n - c(\alpha)t_{n-k+1}}{1 - c(\alpha)} \tag{5}$$

where

$$c(\alpha) = \left(\frac{k}{-\log\alpha}\right)^{-\hat{\nu}} \tag{6}$$

We looked at two levels of certainty: 95% and 80%. Variations in the sighting rate reflect variations in both 'sightability', which may be connected to abundance, and sighting effort (though the latter is not addressed in this study). The main assumption of the technique is that while sighting effort may vary, it never falls to zero over an annual time step, particularly around the time of extinction (Roberts & Solow, 2003; Solow, 2005).

In this study, we addressed two key concerns: (1) missing data and (2) sensitivity to abundance decline trajectory.

1. Sightings records may be incomplete for a number of reasons: sightings may be missed during collection, older sightings might be less likely to be reported (because of there being less people and less of an interest in recording biological observations) and are more likely to be missed during data collation (because older literature is more difficult to access). To test the effect of missing data, sightings for the Greater Bilby (*Macrotis lagotis*, the most data-rich species in this study) were analysed in two ways. To test the impact of missing older sightings, extinction estimates were generated using the four most recent sightings of the 18 available. Next, the five most recent sightings were taken, and the same process followed, stepping back through the data set until all 18 sightings were used. Secondly, the oldest four sightings were analysed with the aim of assessing from the first n observations, whether there was extinction with 95% certainty before the n+1th observation (Type I error). Next, the five oldest recent sightings were taken, and the same process followed, stepping forward through the data set until all 18 sightings were used. To test the impact of missing the sighting during data collation, we rarefied the full data set to ten dates selected at random and calculated the estimated date of extinction. This was repeated 10,000 times, and the mean inferred date of extinction compared with the estimate from the full data set.

2. Decline in abundance may take different forms, each of which may impact the resulting sighting record of a species.

We evaluated how sensitively Type I and Type II error rates depend on the type of underlying decline in species abundance. We simulated four different types of decline in population size: linear, step function, exponential and accelerating declines. We started with a population of 1000 individuals, which was made to decline at rates according to the above curves. Across the decline curve, each individual was assigned a number at random generated from a uniform distribution. We then selected the 7 years with the highest random numbers (which will tend to be those with the larger populations). We thereby generated a sighting record for each decline model, ending with its extinction, which we controlled at 100 years.

Using 1000 runs of the above simulations, we evaluated the Type I and Type II error rates in two ways. First, we evaluated Type I error as the frequency with which from an OLE analysis of the first seven sightings (the mean across the species data set), you would wrongly conclude that the species was extinct at 100 years. We also did this based on the upper 95% confidence limit. For Type II error, we evaluated the frequency with which from an OLE analysis of the first seven sightings, you would wrongly conclude that the species was still extant, when it was actually extinct (at 100 years plus a reasonable period to search – 20 years).

Extinction dates were estimated for the 10 Asian birds and 10 Australian mammals. Confidence limits surrounding these estimates were calculated. All analyses were implemented using R version 2.8.1 (R Development Core Team, 2006).

RESULTS

For the purpose of clarity, hereafter we distinguish between species where the estimated date of extinction is in the past (estimated extinct) and those for which the upper 95% CI estimate is in the past (probably extinct).

Tests of robustness

Running the data sequentially backwards from the most recent four sightings for the Greater Bilby showed that while 95% confidence limits are wide with few data points, the estimated date of extinction becomes consistent with the use of five data points (Fig. 1) and remains so up to 18 data points (the full data set) with 95% CIs becoming progressively narrower. Assessment of Type I error rate (rejecting the null when it is true) showed the technique inferred probable extinction of the species before it was next sighted at two points in the data set (Table 1) if only the estimated date of extinction were considered. However, 95% confidence intervals were never exceeded. Rarefaction of the Greater Bilby data also showed congruence between rarefied data and the full set of dates (Fig. 2). The mean date of extinction estimated from 10,000 repetitions of rarefied sets was the same as the estimated date from the full set (1947). Median estimated date of extinction was higher – 1949. Because of the clear relationship between the number of sightings and the magnitude of confidence intervals as shown in Fig. 1, we also conducted three additional simulations to examine the impact of data distribution (see Appendix S1). We looked at time between penultimate and last observation, total number of observations in a time series and spread of observations within a time series. While estimates of extinction dates extend linearly with all simulations, larger time gaps between second last and last sighting, and increasing the size of all time gaps lead to the upper confidence limit slowly increasing in magnitude (see Appendix S1). We also examined sensitivity of the method to Type I and II errors to varying types of underlying decline in the species abundance (Table 2; see also Fig. S4). Both Type I and Type II errors are high under exponential, accelerating and to a lesser extent linear declines in abundance, and less so under a step function.

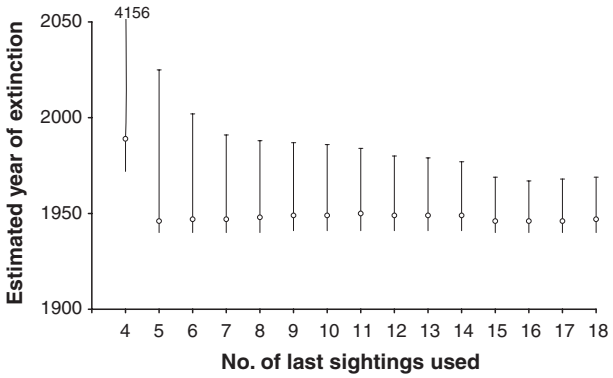

Figure 1 Forward run of data sequence for *Macrotis lagotis* data set, starting with the oldest four sightings. Bars are 95% confidence limits.

Table 1 Evaluation of Type I error rate. Date of extinction sequentially estimated for each successive number of sightings starting from the most distant. Discrepancy represents the difference between estimated date of extinction and the year of next sighting, so negative values suggest Type I error.

No. of sightings	Estimated date of extinction	Year of next sighting	Discrepancy	Upper 95% CI
4	1975	1879	96	7338
5	1948	1883	65	2789
6	1899	1886	13	2012
7	1895	1893	2	1948
8	1904	1896	8	1957
9	1903	1898	5	1937
10	1902	1898	4	1925
11	1899	1899	0	1909
12	1900	1908	−8	1909
13	1913	1912	1	1934
14	1916	1932	−16	1935
15	1946	1932	14	1989
16	1935	1932	3	1949
17	1933	1932	1	1939
18	1947	1940	7	1970

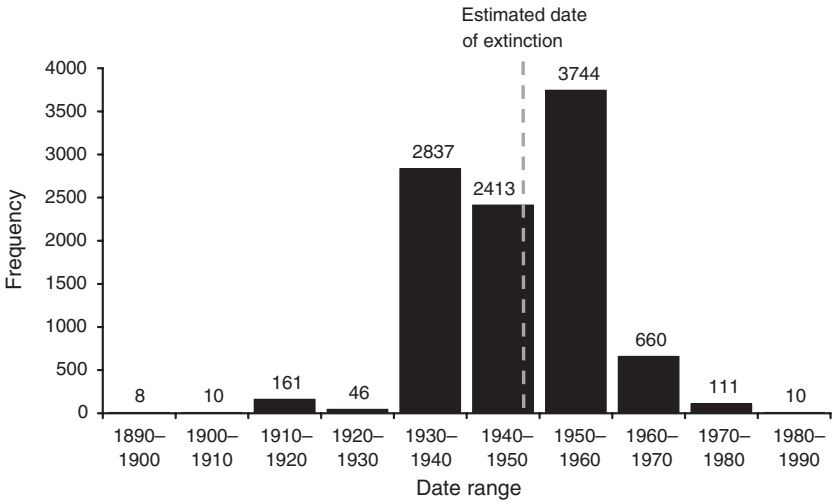

Figure 2 Distribution of estimated extinction dates from 10,000 repetitions of the *Macrotis lagotis* data set, rarefied to 10 data points selected at random. Dotted line is the estimated extinction date from the full data set (1947). Mean estimated date of extinction from randomization test = 1947, median value = 1949.

Table 2 Impact of different abundance decline trajectories on Type I and Type II error. All percentages derived from 1000 runs.

Error type	Linear decline (%)	Exponential decline (%)	Step function (%)	Accelerating decline (%)
Type I – OLE estimate	65.4	93.5	50.9	64.3
Type I – OLE 95%	6.6	47.5	4.8	5.2
Type II OLE estimate	18.5	2.2	22.9	24.0
Type II OLE 95%	0.0	0.0	0.0	0.0

Estimating date of extinction

The most recent sighting of a regionally extinct mammal included in the New South Wales data set was 1940. Using Cooke's estimator, all species except the Bridled nailtail wallaby (*Onchoglea fraenata*) were inferred to be extinct (Table 3), based on estimated date of extinction. The upper 95% confidence limits were often wide, however, such that only the greater Bilby (*Macrotis lagotis*) and the Fawn hopping mouse (*Notomys cervinus*) were inferred to be extinct with 95% certainty (probably extinct). At an 80% confidence limit, five species predicted to be probably extinct (*M. lagotis*, *Chaerops ecaudatus*, *Perameles bougainville*, *N. cervinus* and *Pseudomys gouldii*), three not extinct (*Bettongia penicillata*, *O. fraenata* and *Lagorchestes leporides*).

Seven species of Asian birds have estimated dates of extinction before the present day (estimated extinct: Table 4), four of them significantly so (probably extinct: upper 95% CI also precedes present day: *Columba argentina*, *Ophrysia superciliosa*, *Rhodonessa caryophyllacea* and *Vanellus macropterus*). At a confidence limit of 80%, Rueck's Blue-flycatcher (*Cyornis ruckii*) was also predicted to be probably extinct. Both the White-eyed River-martin (*Eurochelidon sirintarae*) and Sulu Bleeding-heart (*Gallicolumba menagei*) had upper 80% confidence limits within the next four decades, so are predicted to still be extant. For two species (*Otus siaoensis* and *Ptilinopus arcanus*), there was only one record, the type specimen of the species, therefore Cooke's estimator could not be implemented.

DISCUSSION

Superficially, determining whether a species is extinct might seem a simple task, whereby we either find a species to be extant or it is extinct. However, not only do extinct taxa reappear (e.g. Lowe's servaline genet, *Genetta servalina lowei*;

Table 3 Estimated dates of extinction for 10 species listed as Regionally Extinct in New South Wales (NSW Department of Environment & Conservation, 2005). Lower CIs are the calculated values and are not truncated.

Species	Date of last sighting	Estimated date of extinction	95% CIs	80% CIs	No. of sightings
Bettongia penicillata	1906	1963	1971, 4032	1933, 2197	4
Bettongia leseuer	1879	1919	1896, 2986	1901, 2037	4
Macrotis lagotis	1940	1947	1940, 1969	1940, 1957	18
Onchoglea fraenata	1900	2059	1979, 8542	2020, 2848	7
Chaerops ecaudatus	1857	1879	1863, 2686	1867, 1970	8
Perameles bougainville	1857	1876	1857, 2680	1860, 1955	4
Notomys cervinus	1845	1845	1845, 1927	1845, 1848	4
Pseudomys gouldii	1858	1862	1858, 2071	1858, 1882	4
Leporillus conditor	1883	1921	1897, 2193	1906, 2032	4
Lagorchestes leporides	1890	1948	1925, 2437	1943, 2160	6

Species	Date of last sighting	Estimated date of extinction	95% CIs	80% CIs	No. of sightings
Columba argentina	1931	1934	1931, 1951	1931, 1940	9
Cyornis ruckii	1918	1923	1918, inf	1918, 1979	3
Eurochelidon sirintarae	1986	1995	1987, 2326	1988, 2029	4
Gallicolumba menagei	1995	1997	1995, 2650	1995, 2055	3
Ophrysia superciliosa	1876	1880	1876, 1923	1876, 1893	6
Otus siaoensis	1866	Only specimen	–	–	1
Ptilinopus arcanus	1953	Only specimen	–	–	1
Rhodonessa caryophyllacea	1949	1952	1949, 1963	1949, 1957	18
Tadorna cristata	1964	2045	1986, 2869	2003, 2294	5
*Tadorna cristata**	1987	2004	1987, 2116	1989, 2044	7
Vanellus macropterus	1940	1941	1940, 1949	1940, 1944	16

Table 4 Estimated extinction dates for 10 Asian bird species for which the Critically Endangered Possibly Extinct [CR(PE)] framework has been trialled, with limited sightings records, but for which there is a reasonable possibility they might be extinct (Butchart *et al.*, 2006). * = two sightings added – see Appendix S1. Lower CIs are the calculated values and are not truncated.

Brink *et al.*, 2002), knowledge remains sufficiently poor that new species are still being discovered, even in well-studied taxa such as primates (Jones *et al.*, 2005; Sinha *et al.*, 2005).

Cooke's estimator seems to offer a partial solution to help determine extinction in reasonably well-known taxa. For species with sufficient data (>5 sightings), it is a useful tool to assess likelihood of both regional and global extinction. For species with few sightings, the upper confidence limits generally extend so far in the future that they are unhelpful in any assessment of extinction date. There are other potential problems because the technique has the implicit assumption that recording effort never falls to zero and ignores factors other than abundance that influence sightings rate (McPherson & Myers, 2009). However, for comparisons among similar species, these concerns may be relatively minor and outweighed by a consistent and explicit method.

The technique is not useful for species with few sightings. Two percent of mammals listed by IUCN as Critically Endangered (CR) are known only from the holotype and 11% known only from their type locality (Fig. 3). For these species, there is no substitute for further survey work and taxonomic re-evaluation. This lends a particular urgency to the study of their extinction risk that is an entirely separate activity from the probabilistic assessments based on observations. Compared to many other taxa, mammals are relatively well known; estimation of extinction risk is likely to be even harder in most other groups.

Cooke's estimator is designed to consider presence data only and requires a certain number of data points to work usefully. There are pitfalls if the assumptions about sampling of sightings are not met. Consider a hypothetical situation of two point endemics known only from the holotypes – one in the remote Trans-fly region of Papua New Guinea and the other in a regularly visited site such as Regent's Park London. Our conclusions about the status of the species ought to be different simply because the information about non-sightings means very different things in the two locations. The technique would be far more trustworthy if it considered the history of specimen collection or sightings from the same location while retaining optimal linear estimation's robustness. Further, its sensitivity to temporal and spatial variability of search effort within a species range requires further investigation. In cases where there are longer sightings records, new approaches such as those proposed by McPherson & Myers (2009) might be

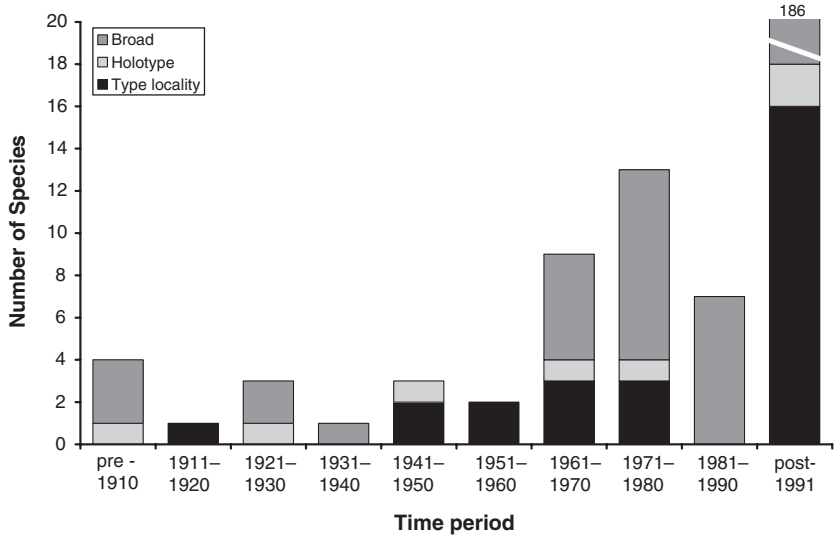

Figure 3 Distribution of most recent sighting date for the 246 mammalian CR species and subspecies (IUCN, 2009). Black = species only known from type locality, light grey = species only known from holotype, dark grey = species found more broadly. Data from M. Hoffmann, unpublished – collected as part of the Global Mammal Assessment (Schipper *et al.*, 2008).

more appropriate. Their technique allows the user to explore how populations of species decline while the organism is still extant, as contrast to confirming extinction.

Analysis of sensitivity under different abundance decline scenarios shows the technique has high Type I and Type II errors with both linear and precipitous declines. Since threats to biodiversity tend to intensify within regions, we are probably in a world of accelerating population decline (Boakes *et al.*, 2010). Type I error rate is also high when a series of sightings occur close together, followed by a relatively long gap before the next, e.g. because of a gap in effort or a local extinction and subsequent recolonization event. In such cases, additional information on sighting effort could be informative. If the intervening period is one of no collection, then the model assumptions are not met. One possibility raised by McCarthy (1998) is that rather than years, each interval could be a time period over which effort is roughly equal so that zero-effort does not occur. Serendipitous observations are always possible to test such ideas.

To tackle the problem of misidentification of extinct species in the Red List, Butchart *et al.* (2006) proposed a Critically Endangered Possibly Extinct (PE) subcategory, which is used to flag CR species that are likely to be extinct, but for which there is a small chance they may still be extant. To make better use of what is often the only available data, techniques such as Cooke's estimator may be useful in addition to the framework developed for the PE category. To be reasonably robust, the methods should be applied to species that have been surveyed to some minimal level, and care taken not to apply the methods and compare results, across very diverse situations. Suitable surrogates for sightability (e.g. related taxa) and search effort (e.g. same region) could be investigated across species.

Incorporation of effort metrics

One of the main concerns over techniques such as Cooke's estimator is how they deal with variation in collection effort. The advantage of this method is that it explicitly does not assume sighting effort is a constant process of equal effort. Variations in sighting rate reflect variation in the 'sightability' of the species, which may be connected to abundance, activity timing, habitat preferences and variations in sighting effort. It is difficult to assess whether the basic assumption that effort does not fall to zero, particularly around the time of extinction (Solow, 2005), is ever the case with early records such as those for New South Wales mammals. In certain areas, retrospective evaluation by constructing oral histories with local communities (Burbidge *et al.*, 1988) can give a greater degree of accuracy of sighting rates for species that were rare early in their sighting record. However, the 'non-zero' assumption means that Cooke's estimator cannot be used with most museum archives because some years saw no collecting effort. Regardless, larger gaps in the sighting record will lead to a more conservative estimate of date of extinction. There must be greater awareness of the desired level of certainty that one is willing to accept, and in cases where it is clear the assumptions are not met, additional survey work must be used instead. Evaluation of sightings records could be combined with information on probable distribution (e.g. Raxworthy *et al.*, 2003) to target comprehensive surveys.

Reed (1996) highlights the problems of statistical inference in balancing the costs of Type I and Type II error. For Type I error (concluding extinction when the species is extant), the cost to be weighed up is that further development (e.g. converting habitat to an alternative use where it is believed the species is no longer present) could ultimately precipitate the actual extinction of that species. The cost is determined by the ability of a species to increase from low population levels, something that evidence suggests is likely to be related to reproductive output, population size and density and speed of life history (Forsyth *et al.*, 2004). Species with traits indicative of a slow life history are likely to fare worse (Purvis *et al.*, 2000b; Cardillo *et al.*, 2005). The cost of Type II error would be continuing to search for a species that is now extinct; the misallocation of limited funds. The direct impact of this could be ameliorated by priority-setting regions, rather than species, focussing searches on areas where there is most uncertainty.

There are several ways forward for estimating extinction. Parallels can be drawn between identifying extinct species and recent work on the eradication of invasive alien species in invasion ecology (van Kleunen & Richardson, 2007). Cross-fostering ideas between the two disciplines may lead to further advances. Several different methods for inferring extinction have been proposed (Smith & Weissman, 1985; Solow, 1993; Burgman *et al.*, 1995; McCarthy, 1998; Hall & Wang, 1999; McPherson & Myers, 2009). The advantage of Cooke's estimator is that it is better able to place an upper bound on the confidence interval than, for example, likelihood (e.g. Smith & Weissman, 1985) or minimum distance approaches (e.g. Hall & Wang, 1999), though it could certainly be used in conjunction with other methods that are sensitive to different characteristics of the collection record. Although this method only uses a limited set of data and should not be used as a sole indicator of extinction, it could be used in conjunction with other available quantitative and qualitative information.

CONCLUSIONS

Ultimately, the IUCN Red List EX and CR (PE) categories could be altered to reflect a range of certainties (Master, 1991; Keith & Burgman, 2004) so that uncertainties are more transparent and threatened and extinct species lists are buffered against changes in knowledge. It might be feasible for example that CR (PE) could include >50% chance, and >95% chance, if we had faith in the statistical method. Accounting for bias because of change in knowledge rather than actual change in status and accurately diagnosing extinction will become increasingly important as we use change in biodiversity patterns to assess key objectives, such as the 2010 target (Butchart *et al.*, 2004, 2005; Balmford *et al.*, 2005; Mace & Baillie, 2007; Collen *et al.*, 2009). Techniques such as the one trialled here, will be most appropriate in

controlled settings, for example where large NGOs or Governments, have control over data quality and can make decisions on thresholds to use, and even send out survey teams.

If the aim is a list of truly extinct species, a stringent criterion for listing is required, so using the 95% CI from a technique such as this is appropriate. This will not be an accurate list of extinct species because many truly extinct species might be missing from it; the risk rate of false positives inferred from the abundance decline scenarios is troubling though. If, however, the aim is to estimate the extinction rate from how lists change in length through time (for example as a technique for monitoring the fate of biodiversity), the most direct way to do that would be to use the median or mean extinction date, on the basis that species whose mean extinction date is in the past are (if the method is unbiased) probably extinct. The ramification of this is that 'extinct' species will often reappear, but there will be a less biased estimate of extinction rate overall.

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Appendix S1 Simulations of data structure variation.

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